# DESCRIPTION OF THE IMMATURE STAGES OF METHONA CONFUSA CONFUSA BUTLER, 1873 AND METHONA CURVIFASCIA WEYMER, 1883 (NYMPHALIDAE, ITHOMIINAE) FROM EASTERN ECUADOR 

Ryan I. Hill<br>Department of Integrative Biology, 3060 Valley Life Sciences Building, University of California, Berkeley, CA 94720;<br>email: rihill@berkeley.edu

AND
Luis A. Tipan
La Selva Jungle Lodge, Mariana de Jesús E7-211 y Pradera, Quito, Ecuador


#### Abstract

Here we describe the complete life history for Methona confusa confusa Butler, 1573 and Methona curvifascia Weymer, $185: 3$ from eastern Ecuador. Each stage from egg to pupa is described and illustrated. Descriptions of first instar chactotaxy and instar durations are also reported. Both species were found feeding on Brunfelsia grandiflora schultesii Plowman. Mature M. confusa larvae have 12 transverse bands that are all yellow in color, including one on segment $A 9$ as observed for M. megisto and M. themisto. In contrast, M. curvifascia lacks a transverse band on segment A9, having 11 transverse bands in total that are white in middle segments and orange in anterior and posterior segments. The pupa of $M$. confusa and $M$. curvifascia differs in the arrangement of spots on the thorax dorsum.


Additional key words: Brunfelsia grandiflora, chaetotary, egg clustering, Solanaceae.

Butterflies in the genus Methona Doubleday, 1847 (Ithominae) are large, warningly colored butterflies illustrated in the original descriptions of both Batesian (M. confusa) and Müllerian (M. megisto) mimicry (Bates 1862; Müller 1879). Despite being involved in the conception of a theory that has generated a massive publication record, Methona biology is relatively poorly understood. The genus Methona is distributed across much of South America east of the Andes reaching its southern limit in southern Brazil, extreme northern Argentina and Uruguay (Forbes 1943; Mielke \& Brown 1979; G. Lamas pers. comm.). In addition, Lamas (2004) indicates that two new subspecies of M. confusa are present in Panama.

Host records have been published for four of the seven recognized species and Methona are apparently monophagous on the Solanaceae genus Brminflsia (Brown 1987; Drummond 1976, 1986; Drummond \& Brown 1987). However, only three species have any published information on immature stage morphology (Brown 1987; Brown \& Freitas 1994; Drummond 1976; Motta 2003; Willmott \& Freitas 2006), and a complete description of the immature stages has not been published for any species in the genus. Here we report on the immature stages of two species of Methona from the upper Amazon basin in eastern Ecuador, Methona confusa confusa Butler, 1873 and M. curvifascia Weymer, 1883. Both of these species are residents of the Amazon basin, however M. confusa is distributed more broadly, occurring throughout the whole basin (and including the populations in Panama mentioned
above), and M. curvifascia is restricted to western Amazonia (G. Lamas pers. comm.). We describe all early stages, report instar durations and provide detailed description of first instar chaetotaxy and briefly discuss differences in larval color pattern in the genus.

## Materials and Methods

Observations were made from Jannary to February 2007 in Provincia Sucumbios, Ecuador, in the forests surrounding Garzacocha ( $00^{\circ} 29.87^{\circ} \mathrm{S}, 76^{\circ} 22.45^{\circ} \mathrm{W}$ ) and Challuacocha ( $00^{\circ} 26.29^{\circ} \mathrm{S}, 76^{\circ} 16.81^{\circ} \mathrm{W}$ ). Early stages were reared in plastic cups and plastic bags under ambient conditions ( $22-30^{\circ}$ C, $70-100 \%$ relative humidity) in a wood building with screen windows. Larvae were moved daily to a shaded environment under a nearby building to maintain ambient conditions. Observations were recorded daily and head capsules and pupal exuviae were collected. Larval specimens were boiled and subsequently stored and studied in $70 \%$ ethanol. Vouchers are deposited in the Essig Museum of Entomology at UC Berkeley. Descriptions other than first instar chaetotasy are based on several individuals from a single clutch of eggs for M. confinsa, and more than 10 individuals for M. curvifascia. First instar chaetotaxy follows nomenclature of Motta (2003), and IIinton (1946), Kitching (1954) and Peterson (1962) were also consulted. The number of specimens for which first instar chaetotaxy was examined is listed in Appendix 1. Host plant vouchers are deposited in the University and Jepson Herbaria at UC Berkeley (voucher number RIH-1424, UC accession \#

UC1933451) and Herbario Nacional de Ecuador (voucher number RH01-117).

## Results

## Methona confusa confusa Butler, 1873

Hostplant. Brunfelsia grandiflora schultesii Plowman (Solanaceae), known locally as chiricaspi. The group of M. confusa eggs was found on an individual plant that also hosted eggs of $M$. curvifascia.

Oviposition. Not observed. Eggs occur in large clusters on the underside of fresh but mature sized leaves. One cluster of 46 un hatched eggs (at 1.5 m ) and a cluster of 18 hatched eggs were found. Plants with eggs were $\sim 2 \mathrm{~m}$ tall and located in shaded areas at gap edges.

Egg. Figure 1A. Duration: Unknown. Eggs hatched four days after found in the field. Egg is white, adomed with 9-11 horizontal and 19-22 vertical ridges making many small rounded cells. Mean egg height $=1.23 \mathrm{~mm}$ (s.d. $=0.04, \mathrm{n}=3$ ). Mean egg width $=0.98 \mathrm{~mm}$ (s.d. $0.03, n=3)$. Mean axes ratio (height/width $)=1.26(s . d=0.01, n=3)$.

Ist instar. Figure 1 B \& C. Duration: 3 to 7 days. Mean head capsulc width $=0.77 \mathrm{~mm}$ (s.d. $=0.02, \mathrm{n}=10$ ). Head capsule and thoracic legs are black. Proleg shields are large and black. Anal plate is present and shiny black. Body is covered with short pale setae. Body is widest near the head and tapering posteriorly. Body is dark olive green with palcr olive transverse bands. Body has pale transverse bands with slightly raised ridges within, ridge on A1 \& A2 most pronounced. Larvac eat chamels into the leaf from the margin consuming all layers of the leaf.

Sec Appendix I for description of first instar chaetotary. An additional lateral body seta (Figure 2) was observed on the meso- and metathorax of the two larvae studied compared with the ithomines studied by Motta (2003), including Methona themisto. This seta is assigned to the lateral group in descriptions (Appendix 1) because this keeps other setae consistent with adjacent segments and the lateral group has a third seta in some moth families (Hinton 1946). Thus, the top seta is inferred to be L1 with the middle L2 and most ventral L3 (Fig. 2). Descriptions of characters involving setae L1 and L2 on these segments should be treated with caution, as homology of L1 and L2 may not have been correctly inferred.

2nd instar. Figure 1D. Duration: 4 to 6 days. Mean head capsule width $=1.18 \mathrm{~mm}(\mathrm{~s} . \mathrm{d} .=0.0 t, \mathrm{n}=10)$. Like the previous instar with the following observations: body is brown and transverse bands are dirty white with tints of yellow. Segments T1-A9 have a transverse band making 12 bands total. The transverse band on segments A3-A6 leans slightly to the posterior. The transverse pale band is located in the posterior of each segment except T1, which is pale anteriorly and almost entirely pale. Transverse ridges are more pronounced this instar.

3rd instar. Figure 1E. Duration: 3 to 4 days. Mean head capsule width $=1.69 \mathrm{~mm}$ (s.d. $=0.04, \mathrm{n}=5$ ). Like previous instar with the following observations: body a rich dark brown and transverse bands dirty white first day turning yellow subsequently. Rest on underside of leaf, sometimes with body straight, sometimes curled in a "J" (Fig. 11I).

4th instar. Figure 1F. Duration: 4 to 7 days. Mean head capsule width $=2.50 \mathrm{~mm}(\mathrm{~s} . \mathrm{d} .=0.07, \mathrm{n}=5)$. Like previous instar with the following observations: transverse bands are yellow and slanting slightly toward the posterior. Transverse bands on A3-6 extend farthest ventrally and are not as pointed at their terminus. Transverse band on A9 is smaller than others, extending the shortest distance ventrally. Laterally, rounded protuberances form a fleshy shelf. Transverse ridges run across this shelf ending below it. The transverse ridges are generally located in the anterior of the transverse yellow band on each segment. Spiracle on Tl is located at posterior margin of yellow band, all other spiracles are anterior of yellow band. Body is covered in short pale pubescence.

5th instar. Figure 1G \& H. Duration: 8 to 12 days. Mean head capsule width $=3.39 \mathrm{~mm}$ (s.d. $=0.20, \mathrm{n}=4$ ). Like previous instar with
the following changes and observations: body dark brown, appearing black in some individuals, with yellow transverse bands. Area of yellow transverse band posterior to ridge fades to whitish on segments A3-6. Yellow bands fade slightly laterally. The day before pupating the yellow fades in all bands.

Pupa. Figure 11, J \& K. Duration: 12 days. Pupa is pendant and bent near abdomen tip but not at abdomen-thorax junction. Pupa colored yellow with distinct black marks. Dorsally with two rows of thin black marks that are thinnest near head. Last segment before cremaster has these dorsal marks merged into wide line. Cremaster is black. Spiracles are outlined in thick black marks. Wing pad has costal margin marked with black. Wing pad posterior margin along thorax marked with black that breaks up into dots near spiracles. Center of wing pad has broken black lines. Ventrally is an inverted black mushroom-shaped spot anterior of cremaster that surrounds a pair of black tubercles. Ventrally at edge of wing pad two black marks merge together. Ocular caps marked with black that starts near eye and extends ventrally as a thick line. Ventrally central black marks over legs and black marks near base of antennae. Thorax slightly keeled with three black marks: anterior spot elongate and thickest toward head, middle one elongate and forked, and posterior one an clongate spot that is widest in the middle (Fig. 1J). The extent of dark markings is variable with some individuals with heavier dark markings (Fig. 1J).

Eyes darken one to two days before eclosing. The day before eclosing black and gold appear in wing pad, then wing pad turns black, followed by abdomen. Pupa has unpleasant odor, as does freshly eclosed adult.

## Methona curvifascia Weymer, 1883

Hostplant. Brunfelsia grandiflora schultesii Plowman (Solanaceae).

Oviposition. A female was observed ovipositing on a relatively small host from 11:30-12:30. The plant was $1.25-1.5 \mathrm{~m}$ tall and located in tall secondary growth with bright light but shaded by a thin canopy of leaves. The female flew to host leaves, tapped the upper surface of the leaf, and then would land on these leaves, occasionally opening her wings and antennating the leaf. She did this repeatedly for 40 minutes. She then landed on a leaf at 0.5 m and hung at its edge, curled her abdomen under and laid a single egg on the underside of the leaf. She was obscured from view after laying this egg but remained close to the site where she laid for $\sim 3 \mathrm{~min}$. She then flew to a nearby bird dropping and fed from it. Three eggs were found where she laid the one obscrved, so she may have laid all three in a few minutes although only the one was observed. Two other eggs were found on this plant along with a freshly hatched first instar. Egg placement with respect to the leaf border appeared somewhat variable and not confined to the leaf border, with eggs somctimes being closer to the leaf midvein than leaf border. Leaves chosen for oviposition varied from small younger growth ( $3-5 \mathrm{~cm}$ in length) to fresh nearly full-sized leaves $(8-10 \mathrm{~cm})$. Other plants hosting eggs/larvae were $\sim 2$ m tall and found in shaded areas at the edge of primary forest gaps.

Egg. Figure 3A. Duration: 6 days $(\mathrm{n}=1)$. Mean egg height $=2.05$ $\mathrm{mm}(\mathrm{s} . \mathrm{d}=0.10, \mathrm{n}=3)$. Mean egg width $=1.30 \mathrm{~mm}(\mathrm{~s} . \mathrm{d} .=0.05, \mathrm{n}=3)$. Mean aves ratio (height/width) $=1.58$ (s.d. $=0.07, n=3$ ). Egg is white, widest two-thirds the distance from base but only slightly wider there. Egg adorned with 14-17 horizontal and 26-30 vertical ridges. The horizontal and vertical ridges make rounded cells that merge near the apex. Head capsule is visible at egg apex one day before hatching.

1st instar. Figure 3B. Duration: 3 days $(\mathrm{n}=2)$ to 4 days ( $\mathrm{n}=2$ ). Mean head capsule width $=0.90 \mathrm{~mm}$ (s.d. $=0.03, \mathrm{n}=2$ ). When first hatched body is dark grey with paler grey transverse bands in anterior of T1 and posterior of segments T2-A8 making 11 pale bands in total. Within each pale band is a raised transverse ridge that crosses the dorsum. Body covered in short pale setae. Head capsule black and thoracic legs are black. Proleg shields large and black. Black selerotized anal plate present. Second day and beyond, body dark brown with white to dirty white transverse bands (Fig. 3B). Transverse bands widest dorsally, more narrow laterally. Transverse band on T1


Fig. 1. Methona confusa immature stages. A. Egg clutch. B. First instar, first day with very pale bands, feeding from leaf margin. C. First instar > 1 d old with pale bands. D. Second instars, midmolt first instars and feeding damage. E. Third instar F. Fourth instar. G. Fifth instar: H. Fifth instar in resting position. I. Ventro-lateral view of pupa. J. Dorsal view of two pupae showing range of variation in black markings. K. Dorso-lateral view of pupa illustrating detail near cremaster.
wider than other segments dorsally. Larvae eat little, to more than three quarters egg when first hatched. Larvae feed at leaf margin making chamels into side of leaf (Fig. 3C \& D). See Appendix 1 for description of first instar chaetotaxy.

2nd instar. Figure 3C. Duration: 3 days $(\mathrm{n}=2)$ to 4 days $(\mathrm{n}=1)$. Mean head capsule width $=1.33 \mathrm{~mm}$ (s.d. $=0.03, \mathrm{n}=4$ ). Like previous instar with the following observations: First day, whitc transverse band of T1 and T2 now with yellow tints. Second day and beyond, transverse band on T 1 is yellow and white transverse band on T2 and AS with yellow tints. Raised ridges more pronounced this instar, with Tl less pronounced than other segments. On segments A3-6 the transverse white band bends fonward laterally and ends just above the proleg. Spiracles dark. Spiracle on T 1 surrounded by yellow in posterior of transverse band. Spiracles in other segments located at anterior margin of bands.

3rd instar: Figure 31). Duration: 3 days $(n=6)$ to 4 days $(n=1)$. Mean head capsule width $=2.00 \mathrm{~mm}$ (s.d. $=0.15, \mathrm{n}=8$ ). Like previous instar with the following observations: Body is very dark brown, some individuals appearing matte black. Non-white bands are more orange-yellow this instar. First day, transverse band on T2 and AS more strongly colored than previous instar, and orange-yellow like T1. band on T3-A7 white. Second day and beyond, transverse band on segments T3, A1 (only some individuals), and A7 develops yellow tints. Transverse bands extend farthest toward venter on segments A3-6.

4th instar. Figure 311. Duration: 5 days $(\mathrm{n}=3), 6$ days $(\mathrm{n}=2), 7$ days $(\mathrm{n}=2)$. Mean head capsule width $=2.70 \mathrm{~mm}(\mathrm{~s} . \mathrm{d} .=0.06, \mathrm{n}=$ 12). Like previous instar with the following observations: Transverse band on $\mathrm{T} 1, \mathrm{~T} 2$ and $\mathrm{A} S$ is orange and band on segments $\mathrm{T} 3, \mathrm{~A}, \mathrm{~A} 2$ and A7 is tinted orange this instar. Transverse band on A7 is wider than other bands except for that on T1.

5 th instar. Figure 31. Duration: 9 days $(\mathrm{n}=1), 11$ days $(\mathrm{n}=7), 12$ days $(\mathrm{n}=4), 13$ days $(\mathrm{n}=1)$. Mean head capsule width $=3.70 \mathrm{~mm}$ (s.d. $=0.19, n=6$ ). Like previous instar with the following observations: Head capsule narrows dorsally with two subtle humps and has short dark setae. Clypeus area is pale grey and frontal sutures pale colored. Body is very dark brown appearing matte black in some individuals. Thorax has additional wrinkles between ridges dorsally. Pale body pubescence more pronounced on ridges. Transverse band on $\mathrm{Tl} \& 2$ is orange tuming white just above leg where it ends without tapering. Transverse band on segment T3 is white, tinted with orange dorsally and ends above leg without tapering. Transverse band on A1 \& A2 tinted orange dorsally, and is white where terminates ventrolaterally in narrow point (A1 narrower point than A2). Segments A3-6 with white transverse band that bends slightly to posterior just before terminating on fleshy bulge above proleg. A 7 with white band tinted orange and terminating in rounded point ventro-laterally. As band is orange, but not as bright as $\mathrm{T} 1 \& \mathrm{~T} 2$, and turns white before tapering to a point ventro-laterally. Orange coloration becomes more extensive and white bands on A3-6 darken two to three days before pupating.

Larvae in all instars rest on underside of leaf with head down near where feeding. Larvae tend to feed first at distal end of leaf and subsequently toward leaf base in later instars. Larvae raise thorax off substrate or curl into tight "J" when disturbed.

Pupa. Figure 3E, F, G\& J. Duration: 11 days $(\mathrm{n}=4$ ) to 12 days ( n $=1$ ). Pupa is pendant and bent near abdomen tip but not at abdomenthorax junction. Pupa is yellow and marked with distinct black spots. Black marks develop within a couple hours of pupating. Head and thorax are slightly darker yellow than abdomen and wing pad. Abdomen dorsum with two rows of black marks that become larger and more rounded toward abdomen apex, and merge into thick line on A10. Laterally, abdomen has seven black spots over spiracles that increase in size toward abdomen apex. Lateral abdomen marks not in a straight line, with marks on A3 \& A4 at wing pad margin out of line with the others. Wing pad has three black lines near its center, black spots along its dorsal margin that become lines basally, and black lines along its ventral margin. Ocular caps colored black, with black extending into a line ventrally. Black cremaster. Thorax dorsum has a pair of anterior black spots, a single medial spot near the anterior pair and another spot posteriorly. Venter has rough upside down "T" near
the cremaster that surrounds two black tubercles. Some variation observed in extent of dark spots on the thorax (Fig. 3E \& F).

Eyes become dark one to two days before eclosion, followed by black and yellow visible in wing pad. Pupa becomes nearly black just before eclosing.

## Discussion

Our observations provide several early stage characters useful for distinguishing Methona confusa and M. curvifascia at this site. Larval coloration differs between these two species with M. confusa exhibiting 12 transverse bands similarly yellow in color along the body, whereas M. curvifascia has 11 bands with those in the middle of the body white, and those at either end orange. The pupa of these two species can be distinguished by the black spots on the thorax dorsum. M. confusa's anterior spot consists of a single spot and its middle spot is "Y" shaped, whereas M. curvifascia's anterior spot is split into two small spots and its middle spot is round. Observed variation in the extent of black markings on the pupa is illustrated in Fig. 1J and Fig. 3E\&F and docs not appear to pose problems for identification using the aforementioned pupal characters. M. confusa eggs are laid in clusters and are shorter ( $p=0.002, t=13.1, n=3$, see above descriptions for means) and narrower ( $p=0.001, t=10.7, n=3$, see above descriptions for means) than M. curvifascia. M. confusa eggs are also relativcly more rounded with a lower axes ratio than $M$. curvifascia ( $\mathrm{p}=0.013, \mathrm{t}=8.2$, $\mathrm{n}=3$, see above descriptions for means).


FIG. 2. Schematic of Methona confusa first instar chaetotaxy for meso- and metathoracic segments illustrating additional lateral seta (L3). Arrangement of body setae on other segments for M. confusa otherwise resembles M. themisto (Figure 19.3 in Motta 2003) except for characters 92 and 93 which are described in Appendix 1.


Fig. 3. Methona curvifascia immature stages. A. Egg. B. First instar. C. Second instar on leaf showing feeding damage of young instars. D. Third instar: E. Dorsal view of freshly formed ( $<1 \mathrm{~d}$ ) pupa. F. Dorsal view of pupa exhibiting mature coloration. Note variation in blaek mark on thorax. G. Lateral view of pupa. H. Fourth instar showing feeding position and damage. I. Fifth instar showing resting behavior. J. Ventral view of pupa.

Observations made here also allow comparison of larval morphology within and among Methona species. The M. confusa confusa larvae observed here are similar to the M. confusa psamathc larva figured in Brown (1987). Although it is difficult to sce, the larva in Brown (1957) Figure 8X appears to have a transverse band on segment A9 making 12 transverse bands in total. The presence of a transverse band on A9 in M. confusa is a trait shared with M. megisto and M. themisto illustrated in Brown \& Freitas (1994) and was identified as a synapomorphy of Methona in Willmott \& Freitas (2006)(Table 2, character 49:1). However, M. curvifascia lacks the transverse band on A9 indicating that not all Mcthona have this character. M. curvifascia is placed as the basal Methona specics in a molecular phylogenetic study (Hill unpublished) suggesting that absence of a transverse band on A9 is the plesiomorphic condition, and evolution of the extra band on A9 occurred after M. curvifascia diverged from the rest of the group. Mcthona curvifascia also may be divergent in egg shape with a mean axes ratio observed here just outside of the range indicated for M. themisto (Brown \& Frcitas 1994) and significantly different than M. confusa as mentioned above.

Aside from the characters just discussed, observations made herc are congruent with most of the synapomorphies for Methona larvae listed in Table 2 of Willmott \& Freitas (2006). The pupa of both M. confusa and M. curvifascia exhibit the sharp curve along the dorsum in the posterior half of the abdomen (character 55:1). The following characters, with their states indicated in parentheses, are also the same for $M$. confusa and M. curvifascia as listed for M. megisto and M. themisto in Willmott \& Freitas (2006): 22(1), 54(0), $56(0), 59(1)$.

Willmott \& Freitas (2006) report that M. megisto and M. themisto lay eggs at the border of leaves and this is indicated as a synapomorphy for the genus (table 2 , character 9:1), however observations on egg placement for both Methona species reported here seem to conflict with this character state. M. confusa lay eggs in clusters that covered a large portion of the leaf, including the middle of the leaf (Fig. 1), atthough scoring this species for this character seems inappropriate because of its cluster-laying habit. It is likely that M. confusa lays eggs while resting on the topside of the leaf, but given its cluster laying behavior it would be interesting to confirm this. M. curvifascia oviposition location does not seem confined to the leaf border, although this may be a result of relatively small host leaf size observed here, because on hosts with larger leaves, laying from the leaf top and curling the abdomen underneath would result in eggs placed near the border. Thus, it may be


Fig. 4. Adult Methona reared in this study. A Mate M. confusa dorsum. B. Malc M. confusa venter. C. Femalc M. curvifascia dorsum. D. Female M. curvifascia venter. M. confusa were identified by vein Sc coalescing with R1, presence of dorsal hindwing costal "hair pencils" in females, and male last abdominal tergite not produced and block-like or spinc-likc. M. curvifascia were idcntified by vein Se not eoalescing with R1, absence of dorsal hindwing costal "hair pencils" in females and male last abdominal tergite produced and narrowing into a spine-like process.
useful to re-evaluate this character by focusing more on female oviposition behavior and less on the resulting egg position.
Methona confusa is the first species in the genus to be observed laying eggs in clusters. In addition to the observation here, A. Freitas observed a female Methona in Acre, Brazil laying a cluster of 12 eggs. The female escaped after ovipositing but was likely M. confusa (A. Freitas, pers. comm.). Cluster-laying has been found to be relatively rare in ithomiines, but it is widely distributed across their phylogeny, being present in 12 genera (including Methona) (Brown \& Freitas 1994; Drummond 1976; Haber 1978; Hill 2006; Willmott \& Freitas 2006). Indeed, using the tribal classification of Willmott \& Freitas (2006), only the tribes Tithoreini and Oleriini lack any cluster-laying species. In addition to Methona, the genera Hypothyris, Episcada, Ithomia, and Pteromymia contain cluster-laying species as well as species known to lay eggs singly (Brown \& Freitas 1994; Willmott \& Freitas 2006; Hill pers. obs.). This suggests life history studies on additional ithomiine species could reveal cluster-laying species in other genera presently known to only lay solitary eggs.

Some ithomiine species that are documented laying eggs in clusters also exist in solitary-laying populations, and this may be the case with M. confirsa as well. In contrast to the M. eonfusa immatures studied here, Brown (1987) illustrated a single M. confusa larva from Venezuela suggesting it was solitary. Of course, Brown's (1987) larva could have been part of a cluster of eggs that had dispersed at some larval stage only appearing to be more or less solitary. Larvae studied here were confined to bags and so no observations on dispersal of a larval group were made. It would be interesting to confirm whether M. confusa populations vary in clusterlaying because this would be an additional example of intraspecific variation similar to what has been observed in two other ithomiine species. Gilbert (1969) observed Mechanitis menapis satmrata laying cggs in clusters in Costa Rica, but Drummond (1976) found M. menapis mantinens laying single eggs in western Ecuador: Similarly, Gilbert (1969) reported Hypothyris enelca valora (called H. e. lencania) laying eggs in clusters in Costa Rica, and Drummond (1976) observed H. enclca intermedia (called H. e. peruviana) laying single eggs at Limoncocha. In contrast to Drummond's (1976) observation we have observed $H$. cuclea intermedia laying eggs in clusters at Garzacocha. Such intraspecific variation could be a fruitful area for investigating hypotheses for cluster-laying in ithomines (Clark \& Faeth 1998; Courtney 1984; Haber 1978; Stamp 1980; Vasconcellos-Neto 1986; Young \& Moffett 1979), and indicates the continuing importance of immature stages to understanding ithomiine biology.

## Acknowledgements

We are grateful to the commmities of Sani Isla and Pilche, and to the management and staff of Sani Lodge and La Selva Jingle Lodge for facilitating this work. RIII would like to thank T. Carlson for discussion about Brunfelsia. We thank the Museo Ecuatoriano de Ciencias Naturales in Quito for granting permits, and G. Byrnes, M. Medeiros and two anonymous reviewers for their comments on the manuseript. This work was supported in part by fellowships from the UC Berkeley Department of Integrative Biology and the Margaret C. Walker Fund for teaching and research in systematic entomology.

## Literature Cited

Bates, H. W. I862. Contributions to an insect fama of the Amazon valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society of London. XXIII: 495-566.
Brown, K. S., JR. 1957. Chemistry at the Solanaceae Ithominae interface. Annals of the Missouri Botanical Garden. 74: 359-397. , \& A. V. L. Freitas. 1994. Juvenile stages of Ithominate: overview and systematics (Lepidoptera: Nymphalidae). Tropical Lepidoptera. 5: 9-20.
Clark, B. R., \& S. H. Faeth. 1998. The evolution of egg clustering in butterflies: A test of the egg desiccation hypothesis. Evolutionary Ecology. 12: 543-552.
Courtney, S. P. 1984. The evolution of egg clustering by butterflies and other insects. American Naturalist. 123: 276-281.

Drummond, B. A., III. 1976. Comparative ecology and mimetic relationships of Ithomiine butterflies in eastern Ecuador. Plı.D. thesis. University of Florida, Gainesville.
1986. Coevolution of ithomine butterflies and solanaceous plants. Pp. 307-327. In W. G. D'Arcy (ed.), Solanaceat biology and systematics. Columbia University Press. New York. , \& K. S. Brown, JR. 1987. Ithomiinae (Lepidoptera: Nymphalidae): Summary of known larval food plants. Annals of the Missomri Botanical Garden. 74: 341-358.
Forbes, W. T. M. 1943. The genus Thyridia (Lepidoptera, Ithomiinae). Annals of the Entomological Society of America. 36: 707-716.
Gilbert, L. E. 1969. Some aspects of the ecology and community structure of ithomid butterflies in Costa Rica. Pp. 61-92. In. Organization for Tropical Studies Report, Organization for Tropical Studies.
HABER, W. A. 1978. Evolutionary ecology of tropical mimetic butterflies (Lepidoptera: Ithomiinae). Ph.D. thesis. University of Minnesota.
Hill, R. I. 2006. Life history and biology of Forbestra oliveneia (Bates, 1862) (Nymphalidae, Ithominae). Jonmal of the Lepidopterists' Society. 60: 20.3-210.
Hinton, II. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Transactions of the Royal Entomological Socicty of London. 97: I-37.
Kitching, I. J. I984. The use of larval chaetotaxy in butterfly systematics, with special reference to the Danaini (Lepidoptera: Nymphalidae). Systematic Entomology. 9: 49-61.
Lamas, G. 2004. Atlas of Neotropical Lepidoptera - Checklist: Part 4A Itesperioidea - Papilionoidea. Gainesville, FL, Scientific Publishers.
Mielke, O. H. II., \& K. S. Brown, JR. 1979. Suplemento ao catalogo dos Ithomiidae Americanos de R. Ferreira d'Almeida (Lepidoptera). (Nymphalidae: Ithominae). Centro de Recursos Audiovisuais da UFPr, Curitiba.
Motta, P. C. 2003. Phylogenetic relationships of Ithomiinae based on first-instar larvae. Pp. 409-429. In C. L. Boggs, W. B. Watt, \& P. R. Ehrlich (eds.), Butterflies: ecology and evolution taking flight. University of Chicago Press, Chicago.
Müller, F. 1879. Ituma and Thyridia; a remarkable case of mimicry in butterflies. Proceedings of the Royal Entomological Society of London: xx-xxix.
Peterson, A. 1962. Larvae of insects. I. Lepidoptera and plant infesting Hymenoptera. Edwards Brothers, Inc:, Columbus, Ohio.
Stamp. N. E. 1980 . Egg deposition pattems in butterflies - why do some species cluster their eggs rather than deposit them singly. American Naturalist. 115: 367-380.
Vasconcellos-Neto, J. 1986. Interactions between Ithominae (Lepidoptera: Nymphalidae) and Solanaceae. Pp. 36t-377. In W. G. D'Arcy (ed.), Solanaceae: Biology and systematics. Columbia University Press, New York.
Whllmott, K. R., \& A. V. L. Freitas. 2006. Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization and diversification. Cladistics. 22: 297-368.
Young, A. M.. \& M. W. Moffett. 1979. Studies on the population biology of the tropical butterfly Mechanitis isthmia in Costa Rica. American Midland Naturalist. I0 I: 309-319.

Reeieved 10 Oetober 2007; revised and aceepted for publication 15 April 2008.

Appendix 1. First instar chaetotaxy of Methona confusa and Methona curvifascia. For the reasons given in Hill (2006), characters are listed as text here rather than as states of Motta's (2003) characters. No larval specimens of M. curvifascia were preserved for study of body chaetotaxy. Descriptions of body setae are based on two larvac for $M$. confusa. Descriptions of head, labrum and mandible chaetotaxy are based on two head capsules for $M$ curvifascia and five head capsules for $M$. confusa.

| Character \# of Motta | M. confusa | M. curvifascia |
| :---: | :---: | :---: |
| Head capsulc |  |  |
| 1 | Seta Cl equidistant to frontal and anteclypeal sutures | Seta Cl equidistant to frontal and anteclypeal sutures |
| 2 | Seta C2 nearer to C1 than to a medial imaginary line | Seta C2 nearer to C1 than to a medial imaginary line |
| 3 | Seta C2 same length at C1 | Seta C2 same length at C1 |
| 4 | Seta F1 undoubtedly more dorsal and medial to C2 | Seta F1 undoubtedly more dorsal and medial to C2 |
| 5 | Seta F1 nearer to C2 than it is to coronal bifurcation | Seta F1 nearer to C2 than it is to coronal bifurcation |
| 6 | Seta F1 subtly nearer to frontal suture than to imaginary medial line | Seta Fl subtly nearer to frontal suture than to imaginary medial line |
| 7 | Puncture Fa aligned with seta F1 | Puncture Fa subtly above seta Fl |
| 8 | Distance between Fa punctures subtly longer than distance between Fa and seta Fl | Distance between Fa punctures similar to that between Fa and Fl |
| 9 | Puncture AFa, and setae AF1 and AF 2 all present | Puncture AFa, and setae AF1 and AF2 all present |
| 10 | Puncture AFa slightly medial of line connccting setae AF1 and AF2 | Puncture AFa in line with to slightly medial of line connecting setae AFl and AF2 |
| 11 | Puncture AFa equidistant to setae AF1 and AF2 (or subtly nearer to AF1) | Puncture AFa cquidistant to setae AF1 and AF2 (or subtly nearer to AF2) |
| 12 | Setae AF1 and AF2 similar in length | Sctae AF1 and AF2 similar in length |
| 13 | Seta AF2 subtly above level of coronal suture bifurcation | Seta AF2 subtly above level of coronal suture bifurcation |
| 14 | Distance of seta AF2 to coronal suture same as distance of AFl to frontal suture | Distance of seta AF2 to coronal suture same as distance of AF1 to frontal suture |
| 15 | Puncture Aa below imaginary line connecting AF1 and A2 | Puncture Aa above imaginary line connecting AFl and A2 |
| 16 | Puncture Aa nearer to A2 than to AF1 | Puncture Aa nearcr to A2 than to AF1 |
| 17 | Seta A 3 posterior to imaginary line between stemma iv and Pl ; distance of A 3 to the imaginary line less than distance of A 3 to stemma iv | Seta A3 posterior to imaginary line between stemma iv and Pl ; distance of A 3 to the imaginary line less than distance of A3 to stemma iv |
| 18 | Seta Al slightly closer to stemma i than ii and aligned to slightly above stemma i | Seta Al closer to stemma ithan ii and aligned to slightly above stemma i |
| 19 | Seta A 2 aligned with imaginary line between stemma ii and AFl | Seta A2 aligned with imaginary line between stemma ii and AFl |
| 20 | Seta A3 not much longer in length than A2 and Ll | Seta A3 not much longer in length than A2 and L1 |
| 21 | Puncture Pa ventral to slightly ventral to imaginary line connecting setae A2 and A3. | Puncture Pa ventral to slightly ventral to imaginary line connecting setae A2 and A3. |
| 22 | Puncture Pa nearer to seta A2 than to A3 | Puncture Pa nearer to seta A2 than to A3 |
| 23 | Puncture Pb aligned with, to slightly medial of, imaginary line between setae P1 and P2. | Puncture Pb aligned with, to medial of, imaginary line between setae P1 and P2. |
| 24 | Puncture Pb closer to seta P 2 than Pl | Puncture Pb closer to seta P 2 than P1 |
| 25 | Setae P1 and P2 equidistant to coronal suture | Seta P2 slightly farther from coronal suture than is seta Pl |
| 26 | Setae Pl and P2 same length to Pl slightly longer | Setae P1 and P2 same length to P1 slightly longer |
| 27 | Puncture La much closer to seta Ll than A3, and less than 1/3 distance between L1 and A3 | Puncture La much closer to seta L1 than A3, and less than 1/3 distance between Ll and A3 |
| 25 | Alignment of puncture La and setae L1 and A3 somerwhat aligned to forming a very obtuse triangle | Alignment of puncture La and setae L1 and A3 somewhat aligned to forming a very obtuse triangle |
| 29 | Seta Ol nearly in line with stemmata i and iv, equidistant to ii and iii; Ol slightly closer to iv than i. | Seta Ol nearly in line with stemmata i and iv, equidistant to ii and iii; Ol slightly closer to iv than i |

Appendix 1. Continued

| Character <br> \# of <br> Motta | M. confusa | M. curvifascia |
| :---: | :---: | :---: |
| Head capsule (cont.) |  |  |
| 30 | Angle formed between O2 and stemmata iv and v less than $90^{\circ}$ | Angle formed between O2 and stemmata iv and v less than 90 |
| 31 | Seta O2 equidistant to stemmata iv and $v$ | Seta O2 equidistant to stemmata iv and $v$ |
| 32,33 | Seta O 2 longer than Ol and O 3 , with O 1 and O 3 similar lengths | Seta O 2 longer than Ol and O 3 , with O 1 and O 3 similar lengths |
| 34 | Seta O3 aligned with stemma $v$ and "groove" | Seta O3 aligned with stemmav and "groove" |
| 35 | Puncture Oa ventral (toward antennal socket) to imaginary line between stemma i and seta Al | Puncture Oa ventral (toward antemal socket) to imaginary line between stemma i and seta Al |
| 36 | Puncture Ob aligned to stemma v and O 3 , and forming a triangle with stemma v and O 2 . | Puncture Ob aligned to stemma vand O 3 , and forming a triangle with stemma v and O 2 |
| 37 | Puncture Ob equidistant or nearer to stemma v relative to O 2 , and farthest from O3 | Puncture Ob nearer to stemmav than $\mathrm{O}_{2}$ and farthest from O 3 |
| 38 | SO1 in ventral end of antennal socket so that distance of SOl to end of antemnal socket is less than $1 / 2$ distance between SOl and SO 3 | SOl in ventral end of antennal socket so that distance of SOl to end of antennal socket is less than $1 / 2$ distance between SOl and SO 3 |
| 39 | SO2 ventral to imaginary line connecting stemmata v and vi | SO2 ventral to imaginary line connecting stemmata v and vi |
| 40 | SO 2 equidistant to slightly closer to stemma vi relative to stemmat | SO2 equidistant to slightly closer to stemma vi relative to stemmat |
| 41 | SO3 posterior to line between stemma vi and SO1 | SO3 posterior to line between stemma vi and SO1 |
| 42 | SOa between suture and imaginary line joining SO3 and G1, SOa same distance from suture as Gl | SOa between suture and imaginary line joining SO3 and G1, SOa same distance from suture as G1 |
| 43 | SOa falls on line between SO 2 and nearest point of maxillary (ventral)suture, SOa is subtly closer to the suture than to SO 3 and much closer to the suture than to $\mathrm{SO}_{2}$ | SOa falls on line between $\mathrm{SO}_{2}$ and nearest point of maxillary ventral) suture, SOa is subtly closer to the suture than to SO 3 and much closer to the suture than to SO 2 |
| 44 | SOb near antemal socket; distance of SOb to antennal socket abont $1 / 2$ that of SO3 to antennal socket | SOb near antemmal socket, distance of SOl to antenmal socket about 1/2 that of SO 3 to antennal socket |
| 45 | SOb nearer, to slightly nearer, to SO3 than to stemma vi | SOb nearer, to slightly nearer, to SO3 than to stemma vi |
| 46 | G1 subtly closer to maxillary (ventral suture) relative to groove | Gl erfuidistant to groove and maxillary (ventral) suture |
| 47 | Ga aligued to line joining G1 and O3 | Ga aligned to line joining G1 and O3 |
| 48 | Ga nearer to O3 | Ga nearer to O3 |
| 49 | V1 nearer to "V" group than P2 | V1 nearer to "V" group than P2 |
| 50 | Stemmata all similar diameter | Stemmatat all similar diameter |
| 51 | Similar distance between stemma i, ii, iii and iv | Similar distance between stemmat, ii, iii and iv |
| 52 | Stemma v closer to vi than to iv | Stemma v closer to vi than to iv |
| Labrum |  |  |
| 53 | Seta M2 aligned or slightly basal to L1 | Seta M2 aligned to L1 |
| 54 | M2 aligned, to slightly dorsal, of line between M1 and L,2 | M2 basal to line between M1 and L2 |
| 5.5 | M1 shifted slightly dorsal relative to M2 | M1 aligned to slightly dorsal of M2 |
| 56 | Distance between M1's greater than distance between M1 to M12 | Distance between MI's greater tham distance between M1 to M2 |
| 57 | M2 longer than M1 | M2 longer than M1 |
| 58 | Puncture S located basal to M1 and M2 | Puncture S located basal to M1 and M2 |
| 59 | Puncture S equidistant to M1 and M2 | Puncture S equidistant to $\mathrm{M1}$ and $\mathrm{M}_{2}$ or a little closer to $\mathrm{M}_{2}$ |
| 60 | Angle between the lines that connect M1 and M2, and M1 and the puncture $S$ is $40^{\circ}-70^{\circ}$ | Angle between the lines that connect M1 and M2, and MI and the puncture $S$ is $40^{\circ}-70^{\circ}$ |
| 61 | Punctare equidistant to subtly nearer to M1 and M2 relative to posterior border | Puncture equidistant to $\mathrm{M1}$ and M 2 relative to posterior border |
| 62 | Puncture S basal to widest point of labrum | Puncture S basal to widest point of labrum |
| 63 | M3 on the distal border of the labrum | M3 on the distal border of the labrum |
| 64 | L2 nearer to L1 than L3 | L2 nearer to L1 than L3 |
| 6.5 | L1 level to widest point of labrom | L1 level to widest point of labrim |
| 66 | Less sclerotized region near the labrum notch and to $\mathrm{M1}$ and $\mathrm{M}_{2}$ | Less sclerotized region near the labrmm noteh and to Ml and M2 |
| 67 | Less sclerotized basal patches athsent | Less sclerotized basal patches absent |
| 68 | Intemal booder of the labral lobe smoothly curved | Internal border of the labral lobe smoothly curved |
| 69 | Basal angle of labrum notch obtuse | Basal angle of lahrum notch obtuse |


| $\begin{gathered} \hline \hline \text { Character } \\ \# \text { of } \\ \text { Motta } \end{gathered}$ | M. confusa | M. curvifascia |
| :---: | :---: | :---: |
| Labrum (cont.) |  |  |
| 70 | Ratio of notch length (= depth) to overall labral length (labral lobe to base) ~0.3: ratio of labral notch width, as mcasured between apices of lobes, to labral length $\sim 1.1$ | Ratio of notch length ( $=$ depth) to overall labral length (labral lobe to base) ~ 0.4; ratio of labral notch width, as measured between apices of lobes, to labral length ~ 1.1 |
| 71 | Ratio of labrum width (between Ll's) to length (labral lobe to base) ~ 2 | Ratio of labrum width (between L1's) to length (labral lobe to base) - 2 |
| Mandible |  |  |
| 72 | Fewer than three small molar teeth | Fcwer than three small molar teeth |
| 73 | Incisurs 2 and 3 similar lengths | Incisors 2 and 3 similar lengths |
| 74 | Lateral grooves radiating from each side of 4 th incisor, one on outside more subtle than others. 4 grooves in total | Lateral grooves radiating from each side of 4th incisor, one on outside more subtle than others, 4 grooves in total |
| Body |  |  |
| 75 | No tubercles present on the thorax |  |
| 77 | Average seta length less than segment width |  |
| 78,79 | Crochets arranged in a circle on segments A3-6, but A10 arranged in a semicircle; all crochet lengths similar |  |
| So | Prolegs with more that 14 crockets on average |  |
| 81 | Cervical sclerite absent on XD1 and $\mathrm{XD2}$ and D1 |  |
| S2 | Seta D 1 shorter than $\mathrm{XD1}$ and $\mathrm{XD} 2, \mathrm{XD1}$ and XD 2 are equivalent in length |  |
| \$3,57 | Setae SD2 and SD1 aligned on T1, SD2 shifted posterior of SD1 on T2A , and SD2 shifted slightly posterior of SD1 on A9 |  |
| S4 | On segment T 1 setae L 1 and L 2 slightly dorsal of spiracle with L 2 between Ll and spiracle; on T2 and T3, L2 is at level of abdominal spiracles; on A1As L1 and L2 below spiracle |  |
| 85,91 | Setae D1 and D2 are equivalent lengths |  |
| S6 | Seta SD2 closer to D2 than to SD1 |  |
| SS | Seta SD2 ventral and posterior to D1 and D2 |  |
| 89.94 | Seta SD1 longer than L1 and equivalent to L 2 on segment T 1 ; on $\mathrm{T} 2 \& \mathrm{~T} 3$ setae SD1 and L2 equivalent and shorter than L1 and L3 (which are same length): SD1 equivalent to L1 and L2 on abdomen |  |
| 90 | Seta L2 present on segments TI-AS |  |
| 92 | Seta SD2 and D1 equivalent lengths and longer than D2 |  |
| 93 | SD2 shorter than SD1 on T1; SD2 longer than SD1 on T2 \& T3; SD2 shorter than SD1 on abdomen |  |
| 95 | L1 shoter than L2 on T1; L1 longer than L2 on T2 and T3 with L3 equivalent to L1: L1 and L2 equivalent on abdomen |  |
| 96 | Additional SY seta on A2 only |  |
| 97 | A9 with one less seta (L1 or L2) than A7 and As |  |
| 98 | Epiproct setae D1, D2, SD1 and L1 similar lengths |  |
| 99 | P1 and SP1 setae present on A10 |  |

